

ON THE PURPOSE OF SELECTIVE INNERVATION OF GUINEA-PIG SUPERIOR CERVICAL GANGLION CELLS

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SUMMARY

Preganglionic axons arising from different levels of the mammalian spinal cord make preferential connexions with different classes of superior cervical ganglion cells (Langley, 1892, 1900; Njå & Purves, 1977*a*). For example, preganglionic axons from the first thoracic segment (T1) make relatively strong connexions with ganglion cells activating end-organs of the eye; conversely, axons arising from T4 selectively innervate ganglion cells projecting to the ear. In the present work we have asked whether this selectivity reflects the function of the pre- and post-synaptic cells, an aspect of their respective positions, or some other criterion.

1. End-organs with different functions at the same locus (the eye) respond to stimulation of the same ventral roots; end-organs of a single modality (hairs or blood vessels) at different positions, however, tend to be activated by different spinal segments. Thus the segmental innervation of ganglion cells is correlated with the position rather than the function of post-ganglionic targets.

2. The role of target position in ganglion cell innervation was examined directly by recording from neurones sending axons to different destinations. Superior cervical ganglion cells running dorso-medially in a spinal nerve receive, on average, innervation from more caudal segments than cells projecting ventro-laterally.

3. These selective connexions do not depend on intraganglionic cell position: neurones located at different points along the major axes of the superior cervical ganglion receive, on average, the same segmental innervation. In accord with this observation, retrogradely labelled neurones innervating a particular target such as the eye or ear are widely and randomly distributed within a large portion of the ganglion. Thus the importance of post-ganglionic target position in ganglion cell innervation is not simply a reflexion of ganglionic topography.

4. We conclude that one purpose of the selective connexions in the superior cervical ganglion is to bring together preganglionic axons arising from different levels of the spinal cord and ganglion cells whose axons innervate particular regions of the superior cervical territory.

INTRODUCTION

The synapses that form between preganglionic axons and neurones of the mammalian superior cervical ganglion are selective in that preganglionic fibres arising from different spinal levels contact different classes of ganglion cells. This conclusion

is based on the observation that stimulation of each of the upper thoracic ventral roots supplying innervation to the superior cervical ganglion elicits qualitatively different end-organ effects (Langley, 1892, 1895, 1897, 1900; Njå & Purves, 1977*a, b*, 1978; see also Murray & Thompson, 1957; Guth & Bernstein, 1961). The cellular counterpart of the selectivity inferred from *in vivo* experiments is a broad preference of each neurone for innervation from a contiguous subset (four on average) of the eight ventral roots which contribute innervation to the guinea-pig superior cervical ganglion (Njå & Purves, 1977*a, b*, 1978).

In the present work we explore the purpose of this selective innervation. Such selectivity might match the function of the pre- and post-synaptic cells, an aspect of their respective positions, or some other neuronal property. Our results suggest that segmentally selective connexions between preganglionic axons and ganglion cells depend on positional attributes of the synaptic partners. The relevant position for preganglionic neurones appears to be the level of their emergence from the spinal cord; for ganglion cells the relevant position is that of their post-ganglionic target.

METHODS

Electrophysiological experiments in vivo

We studied the pattern of end-organ responses in the territory supplied by the superior cervical ganglion in response to stimulation of the thoracic ventral roots or, in some cases, of particular post-ganglionic nerves. The techniques used and method of grading responses were similar to those previously described (Njå & Purves, 1977*a, b*, 1978). Adult guinea-pigs (Hartley, 250–400 g) were anaesthetized with pentobarbitone (35–40 mg/kg *i.p.*) and maintained on a respirator. A thoracic laminectomy was performed, the spinal cord removed, and the right ventral roots of T1–T5 supramaximally stimulated in turn for several seconds with a suction electrode (1.0 msec pulses, 50–100 V, 20/sec). The responses of the ipsilateral eye were observed through a horizontally mounted dissecting microscope (10.5 \times); the responses of the hairs of the head and neck were observed without magnification, and the active areas drawn on a standard diagram of the guinea-pig. The responses of blood vessels in the ear (pinna) were also observed through a dissecting microscope. At the end of some experiments the cervical sympathetic trunk was avulsed by means of a fine ligature placed around it during the initial tracheotomy. Stimulation of the fourth or fifth thoracic ventral root was then repeated to ensure that the more caudal hair responses were indeed mediated by the superior cervical ganglion. In additional experiments the cervical trunk was cut at the beginning of the experiment; stimulation of the thoracic ventral roots after trunk section showed the approximate border between the stellate and the superior cervical ganglion to be at level of the upper neck and to overlap by at least a few millimetres.

Electrophysiological experiments in vitro

The superior cervical ganglion (Fig. 1) was dissected in continuity with the cervical sympathetic trunk and the thoracic portion of the sympathetic system and placed in a bath perfused with oxygenated mammalian Ringer fluid at room temperature (see Njå & Purves, 1977*a*, for details). The ventral roots which innervate the ganglion (C8–T7) were stimulated while recording from individual ganglion cells with an intracellular micro-electrode (resistance 80–100 M Ω). In experiments where the segmental innervation of ganglion cells projecting to different positions was assessed, the inferior branch of the superior cervical ganglion was dissected in continuity with the second and third cervical nerves (Fig. 1). Suction electrodes were then applied to each of these spinal nerves both lateral and medial to the junction of the post-ganglionic ramus. The suction electrodes were used both to stimulate antidromically and to record compound action potentials in response to stimulation of the thoracic ventral roots. In further studies the spinal nerve of C3 was dissected with the branches of its major dorsal division (see Fig. 5).

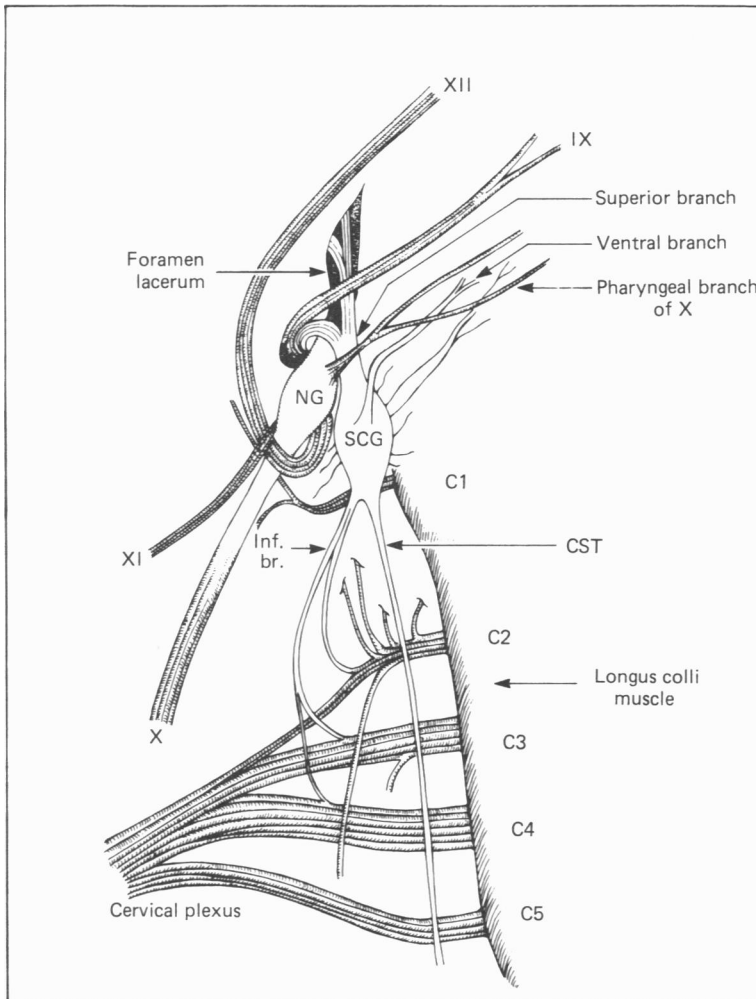


Fig. 1. Diagram of the branches of the superior cervical ganglion (SCG) and the cervical and cranial nerves that they join. CST, cervical sympathetic trunk; NG, nodose ganglion; Inf. br., inferior branch. The superior post-ganglionic branch is actually a group of nerves which separates into two divisions within 2–3 mm of the rostral pole of the ganglion. The lateral division ramifies at the origins of the IXth–XIIth cranial nerves, while the larger medial division traverses the foramen lacerum to join the more rostral cranial nerves. The inferior post-ganglionic branch also divides after leaving the caudal pole of the ganglion, although the two divisions may run together for many millimetres. The more rostral division usually joins the second cervical nerve, while the caudal division joins the third cervical nerve. A small additional branch sometimes runs to the fourth cervical nerve. The ventral post-ganglionic branch usually runs as a single bundle to the vicinity of the carotid bifurcation where it ramifies and follows the blood vessels.

Compound action potentials were then recorded from the secondary branches of the dorsal division while stimulating the thoracic ventral roots.

Retrograde marking with horseradish peroxidase

The distribution of ganglion cells innervating particular targets was determined by injecting 100–200 μ l. of horseradish peroxidase solution (HRP; Sigma Type VI, 5–10% (w/v) in saline)

into the eye or the ear. Injections were made transcorneally into the vitreous of anaesthetized animals, or subcutaneously on the dorsal aspect of the pinna. After 48 hr the animals were re-anaesthetized and perfused through the heart with 0.5 l. of mammalian Ringer fluid. The ipsilateral (and in some cases the contralateral) superior cervical ganglia were removed and fixed for 1 hr in dilute Karnovsky solution (Karnovsky, 1965). The tissues were then fixed in full strength Karnovsky solution for an additional 1 hr and stored in 10 % sucrose/cacodylate buffer. Frozen serial sections (30 μ m) were cut, and the HRP reaction product developed with 0.05 % diaminobenzidine and hydrogen peroxide. Sections were counter-stained with thionine, and examined with dark-field illumination.

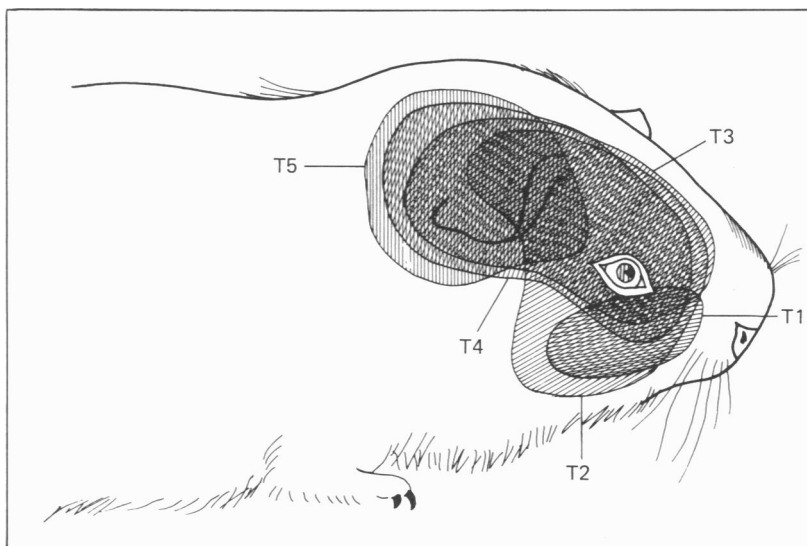


Fig. 2. Areas of piloerection within the territory of the superior cervical ganglion elicited *in vivo* by stimulation of the ventral roots T1–T5. C8, T6 and T7 were not routinely stimulated because these roots contribute relatively little innervation to the superior cervical ganglion. The result shown is similar to that in nine other animals in which this experiment was carried out. In each case stimulation of successively more caudal ventral roots caused piloerection in a widely overlapping but progressively more dorsal and caudal area of the superior cervical ganglion territory. The most caudal ventral root causing piloerection was stimulated again after avulsion of the cervical trunk; the disappearance of all, or a large part, of the response showed that the effect was mediated by the superior cervical ganglion. In seven of ten animals no piloerection was observed upon T1 stimulation, and when a response was present the active patch was always relatively small. The size of the area undergoing piloerection in response to stimulation of each root was quite variable and appeared to be a function of the depth of anaesthesia.

RESULTS

Relation of segmental innervation to the function and position of post-ganglionic targets

The right ventral roots of T1–T5 were exposed and stimulated in ten guinea-pigs while observing the end-organ effects in the territory of the superior cervical ganglion. In each of the animals, stimulation of successively more caudal ventral roots tended to cause piloerection of largely overlapping but progressively more dorsal and caudal areas (Fig. 2). Stimulation of roots separated by several segments (for example T1

and T5 usually gave non-overlapping responses when pilorecction could be elicited from both levels (Fig. 2). Similarly, arterioles in different positions were constricted by stimulation of different ventral roots: vasoconstriction in the iris and sclera was elicited by stimulation of more rostral ventral roots than blanching of the pinna (Table 1). These results show that end-organs of the same modality at different

TABLE 1. Effects of T1 and T4 ventral root stimulation on the eye and the ear in eight different animals (evaluation of responses was subjective; 0 = no detectable response, + + + + = maximum response)

Ventral root stimulated	Vasoconstriction of iris	Pupillary dilatation	Widening of palpebral fissure	Vasoconstriction of pinna
T1	+ + +	+ + +	+ +	0
	+ +	+ + +	+	0
	+ + +	+ + +	+ + +	0
	+ +	+ + +	+ +	0
	+ +	+ + +	+ +	+
	0	+ +	+ +	0
	+ +	+ + +	+ +	+
	+ +	+ + + +	+ + +	0
T4	0	0	0	+ + + +
	0	0	0	+ + + +
	0	0	0	+ + +
	0	0	+	+ + +
	0	0	0	+ + + +
	0	+	+	+ + +
	0	0	0	+ + + +
	0	0	0	+ + + +

positions tend to be activated by preganglionic axons arising from different subsets of the spinal cord segments which innervate the ganglion as a whole (see also Langley & Sherrington, 1891; Langley, 1894).

The sympathetic responses of the eye also allowed us to observe the segmental innervation of post-ganglionic targets with different functions at the same locus. In every animal the same spinal roots caused vasoconstriction in the iris and sclera, dilatation of the pupil, and widening of the palpebral fissure (see Table 1; see also Langley, 1892; Langley & Anderson, 1892; Njå & Purves, 1977a).

Thus end-organs of different modalities at the same locus receive, within the resolution of these techniques, the same segmental innervation, while the same class of end-organs at different locations tends to be innervated by different spinal segments. When end-organs of the same modality are present throughout the territory supplied by the superior cervical ganglion (e.g. hairs or blood vessels) that modality is probably innervated by most or all of the segments providing some innervation to the ganglion. In sum, the location of a ganglion cell's peripheral target is correlated with the segmental innervation the neurone receives.

These results are to some extent expected from intracellular recording in normal ganglion cells (Njå & Purves, 1977a, b; see also below). Since superior cervical ganglion cells are innervated by about four segments on average, end-organs at a particular locus within the territory supplied by the ganglion should be activated by stimulation of several contiguous ventral roots. This

is indeed the case (Fig. 2; see also Njå & Purves, 1977*a, b*, 1978). The gradual and overlapping nature of the shift in the position of segmentally activated fields within the ganglion's territory (Fig. 2) is also in agreement with intracellular observations. For example, neurones in the superior cervical ganglion innervated by preganglionic axons arising from T1 are also innervated by T2 (Njå & Purves, 1977*a*). Thus supramaximal stimulation of T2 should activate most or all of the region driven by T1. There are, however, many cells innervated by T2 but not by T1, cells generally dominated by more caudal segments (see Njå & Purves, 1977*a*). As a result, stimulation of T2 should activate the region driven by T1 plus an additional region responsive to more caudal segments. A similar argument can be made for the other ventral roots contributing innervation to the ganglion.

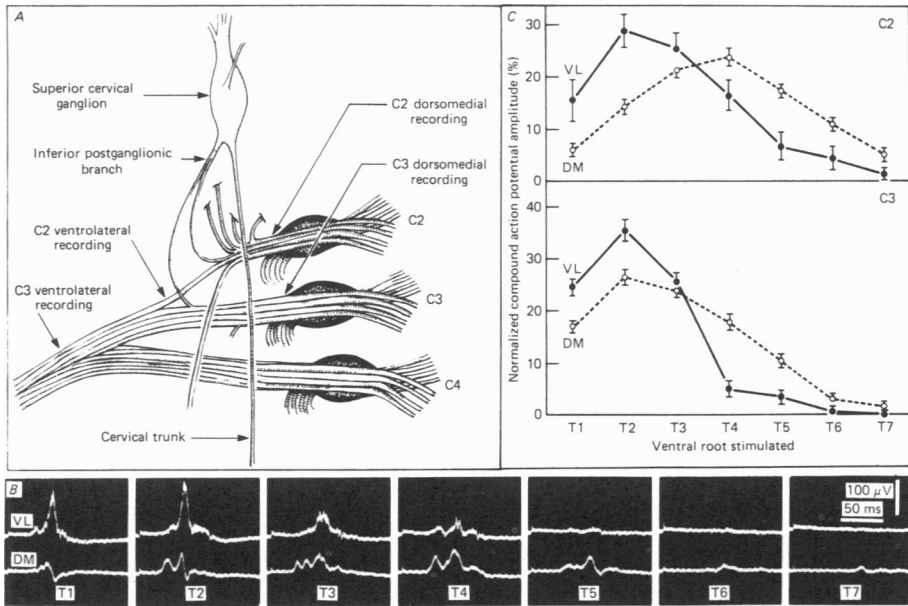


Fig. 3. Compound action potentials recorded *in vitro* from ventrolateral- and dorso-medial-going sympathetic axons in the cervical spinal nerves. *A*, points of recording along the second and third cervical nerves; *B*, compound action potentials simultaneously recorded from C2 sympathetic axons going to different destinations in response to stimulation of thoracic ventral roots. (VL ventrolateral-going; DM, dorso-medial-going). The largest response of the VL axons occurred upon stimulation of T2, whereas T4 activated the largest number of the DM axons. Graph *C*, mean responses of VL and DM axons recorded from C2 and C3 in different animals. Each point represents at least ten normalized determinations (\pm s.e. of mean).

Further evidence for the correlation of segmental innervation and the position of post-ganglionic targets

The foregoing *in vivo* results provide evidence that segmentally selective innervation is correlated with the position of post-ganglionic targets. The accessibility of some post-ganglionic nerves of the superior cervical ganglion (Fig. 1) allowed us to show directly that sympathetic axons running to different destinations arise from neurones receiving systematically different segmental innervation.

The inferior branch of the superior cervical ganglion usually arises as two loosely associated nerves which join the primary ventral divisions of the second (C2) and third (C3) cervical nerves (Figs. 1 and 3*A*). The compound action potentials in response to ventral root stimulation were different for those sympathetic fibres

travelling ventro-laterally in the spinal nerves compared to those axons travelling dorso-medially (Fig. 3*B* and *C*). For both C2 and C3, the largest sympathetic compound action potentials in ventrolateral-going axons were elicited by stimulation of the ventral roots T1–T3, while the compound action potential arising from axons running dorso-medially was proportionally less to T1 and T2 stimulation, and greater in response to stimulation of T2–T5.

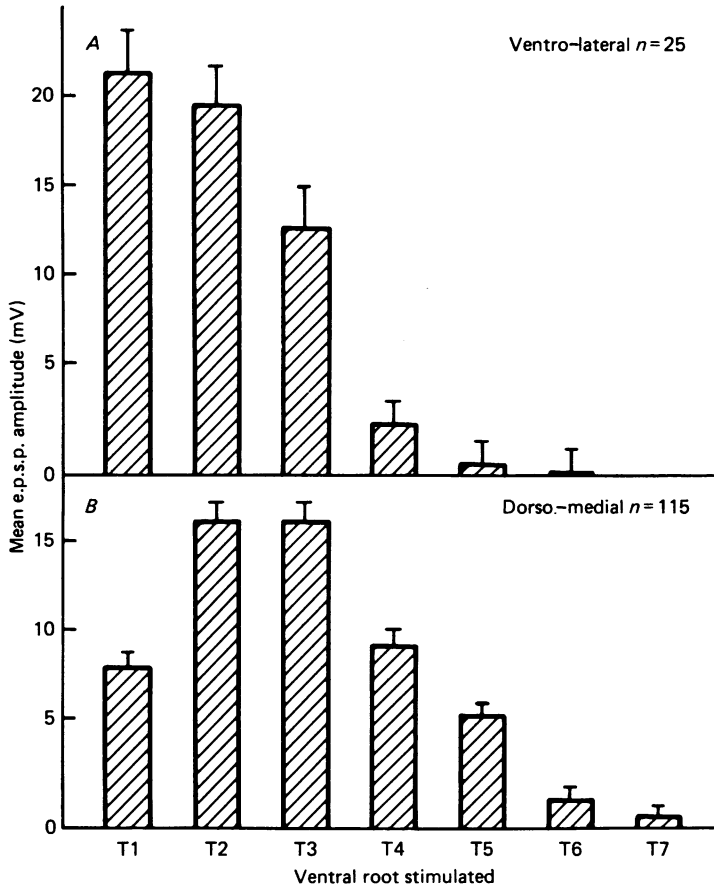


Fig. 4. Distribution of mean e.p.s.p. amplitudes (+s.e. of mean) in neurones antidromically driven from the second and third cervical spinal nerves in response to thoracic ventral root stimulation. Neurones activated from the points shown in Fig. 3*A*. Neurones whose axons ran ventro-laterally (*A*) received more rostral thoracic innervation, on average, than neurones whose axons ran dorso-medially (*B*).

To determine the segmental innervation of individual ganglion cells projecting to different locations, we recorded intracellularly from 200 neurones antidromically driven by either the ventrolateral- or dorsomedial-going sympathetic fibres in C2 and C3 (Fig. 4). In these experiments four suction electrodes were applied to C2 and C3 as indicated in Fig. 3*A*; thus each of the 200 cells impaled was identified as running in one or more of the branches stimulated by the suction electrodes. Only seven of the 200 neurones travelled in both C2 and C3. However, many axons

(sixty out of 200) branched into both limbs of one of the spinal nerves. Those axons that ran only ventro-laterally in either C2 or C3 (twenty-five out of 200) arose from neurones whose segmental innervation was, on average, from rostral thoracic segments (Fig. 4*A*). In contrast, ganglion cells whose axons ran only dorso-medially in

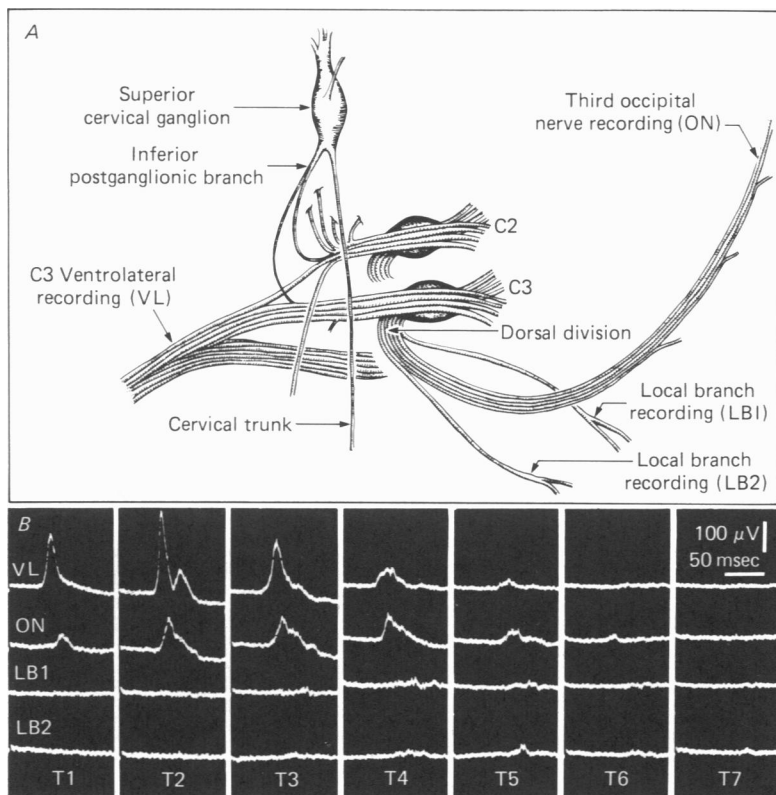


Fig. 5. Comparison of compound action potentials recorded simultaneously from secondary branches of the dorsal division of the third cervical spinal nerve. (*A*) shows position of recording electrodes on the ventrolateral-going nerve (VL), the third occipital nerve (ON), and two local branches (LB1 and LB2) innervating the occipital region. *B*, the innervation of neurones whose axons ran in the local branches arose largely from caudal thoracic segments, while at least some neurones whose axons ran in the third occipital nerve also received rostral innervation. Comparison with responses of ventrolateral-going axons (VL), however, shows that neurones whose axons run in the branches of dorsal division receive generally more caudal thoracic inputs.

the spinal nerves (115 out of 200) received more caudal segmental innervation (Fig. 4*B*). The distribution of innervation to neurones whose axons divided to run in both directions was intermediate to that shown in Fig. 4*A* and *B*. These results show that the segmental innervation of superior cervical ganglion cells is correlated with the dorso-ventral projection of their post-ganglionic axons.

Although the average thoracic input of ventrolateral-going superior cervical ganglion cells was shifted rostrally, there was considerable heterogeneity of the segmental innervation to those neurones whose axons ran dorso-medially. Some dorso-medial-going cells, for example, received dominant innervation from T1 or T2. One

explanation for this observation might be that some cells classified as dorsomedial-going also sent axon collaterals ventrally in one of the branches of the spinal nerves which we did not stimulate (see Figs. 3 and 5). Heterogeneity of inputs might also arise because of the range of axonal destinations at the point of antidromic stimulation. To test this latter idea, we recorded compound action potentials from secondary branches of the dorsal division of C3 (Fig. 5A). In each of the five animals

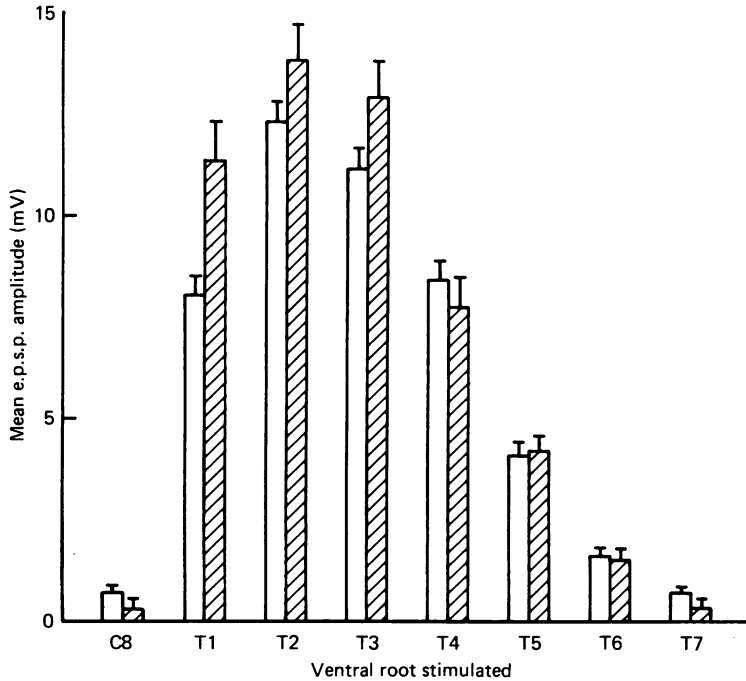


Fig. 6. Distribution of mean e.p.s.p. amplitudes (\pm s.e. of mean) in response to ventral root stimulation in neurones whose axons run in the superior or inferior post-ganglionic nerves. Open bars, neurones antidromically driven by superior branch stimulation ($n = 427$). Cross-hatched bars, neurones antidromically driven by the inferior branch ($n = 116$).

studied we found that the amplitude of the compound action potentials in branches ramifying locally to supply the occipital region was greatest in response to caudal ventral root stimulation (T3–T6). However, the post-ganglionic sympathetic axons in the third occipital nerve, which ramifies somewhat more anteriorly, responded to stimulation of T1 and T2 as well as to stimulation of the more caudal thoracic segments (Fig. 5B). This suggests that the relatively diverse innervation of dorso-medial-going ganglion cells is at least in part the result of a wide range of eventual destinations.

Segmental innervation of neurones running in the inferior and superior branches of the superior cervical ganglion

In the light of the results described in the preceding sections it is surprising that the average segmental innervation of neurones antidromically driven by the superior and inferior post-ganglionic branches is similar (Fig. 6). If the position of

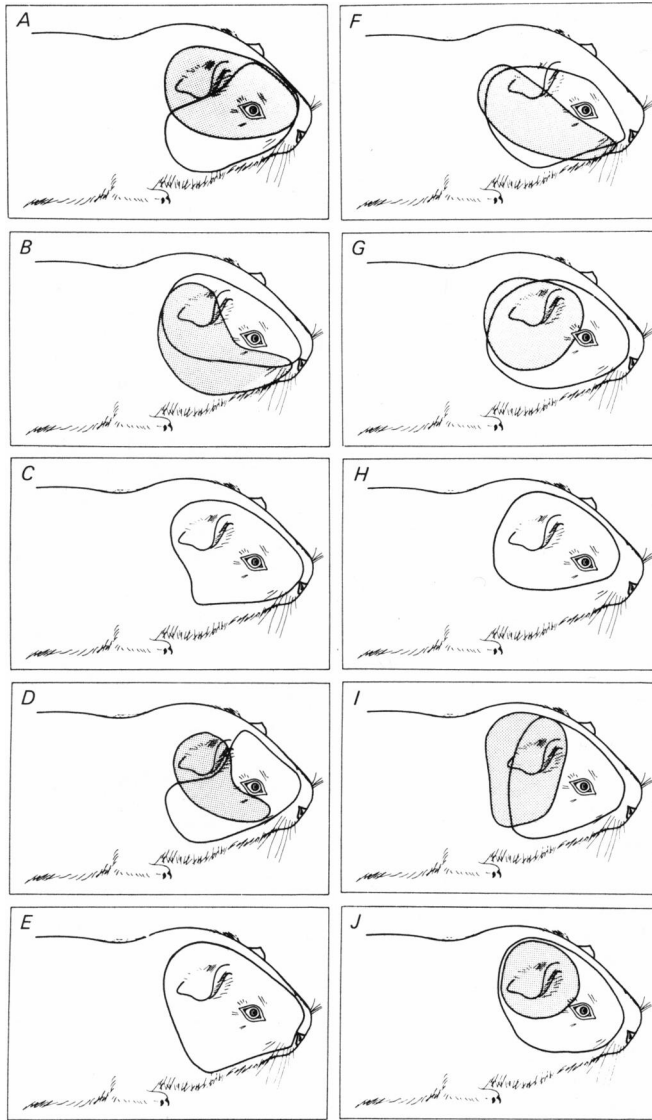


Fig. 7. Areas of piloerection elicited *in vivo* by post-ganglionic stimulation of the superior (open) and inferior (stippled) post-ganglionic branches of the superior cervical ganglion. In most of the ten animals in which these nerves were stimulated the areas of piloerection overlapped widely. In three animals, however, inferior branch stimulation caused no piloerection (*C*, *E*, and *H*). Overlap was also apparent in the innervation of the blood vessels of the pinna. In every animal, inferior branch stimulation caused moderate to marked vasoconstriction of the whole ear; stimulation of the superior nerve also caused vasoconstriction of the ear, but the response was in each case weaker and often limited to the anterior half. End-organs of the eye were always activated by the superior, but not the inferior post-ganglionic branch.

post-ganglionic targets is important, then the similar segmental innervation of inferior and superior branch neurones presents a paradox, since these nerves leave the ganglion at opposite poles and join different peripheral nerves (Fig. 1).

At least two aspects of our results might explain this apparent inconsistency. First, in ten animals in which these two post-ganglionic nerves were stimulated directly, each nerve was found to supply a large and overlapping part of the superior cervical territory (Fig. 7). Thus, although we sampled only effects apparent at the

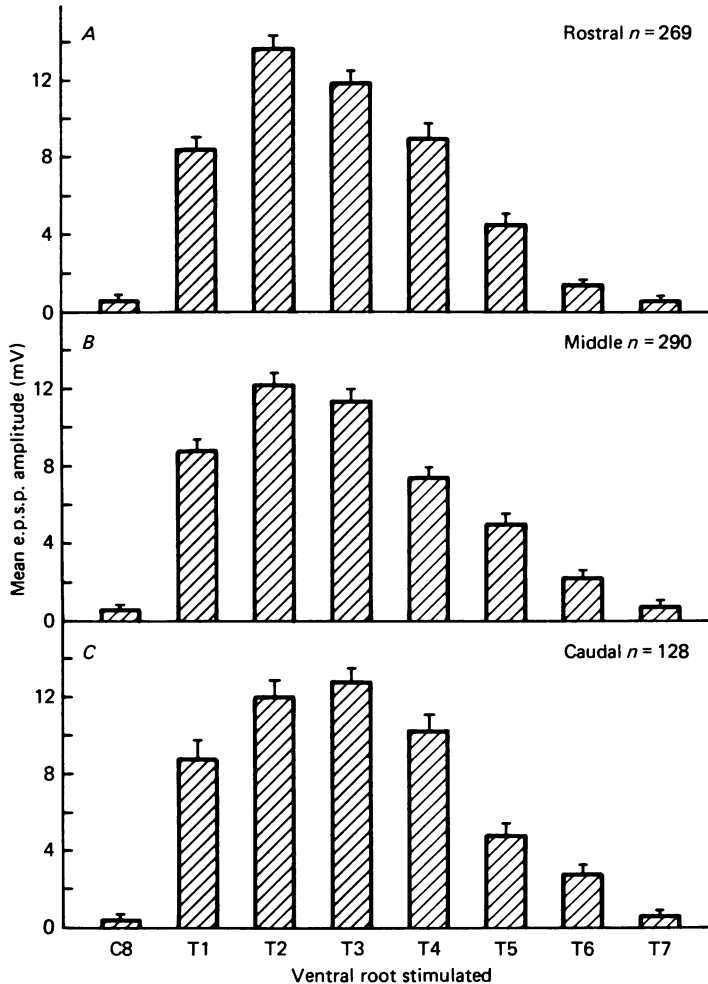


Fig. 8. Distribution of the mean e.p.s.p. amplitudes (\pm s.e. of mean) in neurones located in the rostral (A), middle (B) and caudal (C) thirds of the superior cervical ganglion in response to stimulation of different ventral roots. Ganglion cell position was measured with a micrometer eyepiece and expressed as a fraction of the rostro-caudal length of each ganglion.

body surface, considerable overlap in segmental innervation would be expected. Secondly, one axis of the body may be more strongly correlated with segmental innervation than others. If both inferior and superior branches supplied congruent regions along the relevant axis, then their component neurones would receive similar segmental inputs, even if their respective territories differed in other dimensions.

Position of neurones within the superior cervical ganglion as a factor in the selective innervation of ganglion cells

By analogy with other systems in which the selective innervation of neurones is thought to be based on topography, segmentally selective innervation of ganglion cells might be due to their position within a ganglion. To test this idea, neurones that had been impaled in the superior cervical ganglion were divided into groups according to their position. The average segmental innervation of neurones located at different points along the rostro-caudal axis was similar (Fig. 8). The influence of position along the other major axes was also tested by comparing the inputs to groups of about 100 neurones on the dorsal and ventral surfaces of the ganglion, as well as similar groups along the medial and lateral edges. In neither case was any obvious difference in segmental innervation found.

Although neurones preferring different segmental innervation are not arranged systematically along the major ganglionic axes, intraganglionic cell position might still be important if ganglion cells innervating targets in a particular position were clustered, or grouped in some other way within the ganglion. To examine this possibility, an HRP solution was injected into the right eye in five guinea-pigs, and into the right ear in six others. After allowing retrograde transport of the marker, the position of the labelled cells was determined in serial frozen sections. After either eye or ear injection, labelled neurones were distributed throughout a large part of the ipsilateral superior cervical ganglion (Fig. 9*A* and *B*; see also Hendry, 1977). Labelled neurones were not seen in contralateral ganglia. Cells marked after HRP injection into the eye were scattered randomly (Fig. 9*C*) within a region of the ipsilateral ganglion corresponding to the overall distribution of neurones sending axons into the superior post-ganglionic branch (Purves, 1975; Bowers & Zigmond, 1979; D. Purves, J. W. Lichtman & J. W. Yip, unpublished). This is consistent with the observation that *in vivo* stimulation of the superior branch, but not the inferior branch, causes dilatation of the pupil.

Similarly, cells labelled after ear injection were found throughout the caudal part of the ganglion, the normal location of neurones emerging in the inferior post-ganglionic branch (Purves, 1975). A number of cells, however, were also found scattered throughout the rostral portion of the ganglion after ear injection. This in turn is consistent with the *in vivo* finding that post-ganglionic stimulation of the inferior branch invariably caused strong vasoconstriction of the ear, although weak to moderate effects on the ear were also elicited by stimulation of the superior branch in each of ten animals tested (see above).

Thus in the superior cervical ganglion there is no obvious relation between the intraganglionic position of neurones and the segmental innervation they receive.

Position of preganglionic neurones as a factor in the selective innervation of ganglion cells

One explanation for selective innervation by preganglionic neurones emerging in different ventral roots would be a continuous rostro-caudal gradient of affinity within the cord for ganglion cells projecting to a particular position. An alternative,

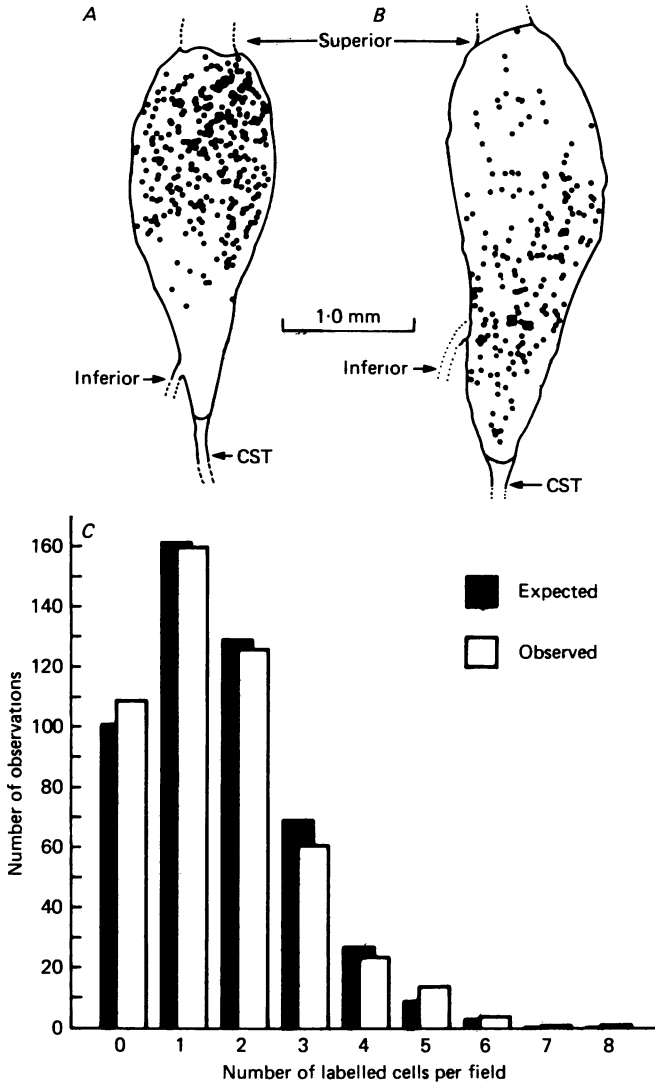


Fig. 9. Camera lucida drawing of typical transverse sections from the mid-region of two different superior cervical ganglia 48 hr after injection of horseradish peroxidase into the ipsilateral eye (A) or pinna (B). Each filled circle represents a labelled neurone. In C the incidence of labelled neurones per oil immersion field (open bars) is compared to the incidence expected if labelled cells occurred at random (dark bars). The expected values were calculated from the Poisson theorem,

$$P_x = \frac{m^x}{x!} e^{-m},$$

where P_x is the probability of x labelled neurones in a particular field and m is the mean number of labelled cells per field. The observations were made on the rostral half of sections from the ganglion which provided the section shown in A. The two distributions are similar; thus although neurones are restricted to a region of the ganglion dictated by their branch of exit (Purves, 1975; Bowers & Zigmond, 1979; D. Purves, J. W. Lichtman & J. W. Yip, unpublished), within this region the position of neurones supplying a particular post-ganglionic location appears to be largely a matter of chance.

however, would be that all the preganglionic neurones contacting a ganglion cell are equally attracted to it. In this case, the increasingly weak connexions made by preganglionic neurones arising from spinal levels progressively more distant from the dominant level (Njå & Purves, 1977a) would be due to progressively smaller numbers of preganglionic neurones with identical affinities for that ganglion cell. To distinguish these alternatives we selected all the superior cervical ganglion cells

TABLE 2. Synaptic contributions of T1 and T4 preganglionic axons to superior cervical ganglion cells innervated by both these segments and dominated by one of them

Neurones dominated by T1, innervated by T4 ($n = 90$) (\pm s.e. of mean; e.p.s.p. in mV)			
T1		T4	
Mean e.p.s.p.	Mean no. axons	Mean e.p.s.p.	Mean no. axons
23.5 ± 0.8	3.2 ± 0.1	6.3 ± 0.7	1.9 ± 0.1
Depolarization/axon = 7.3 mV		Depolarization/axon = 3.3 mV	
Neurones dominated by T4, innervated by T1 ($n = 60$)			
T4		T1	
Mean e.p.s.p.	Mean no. axons	Mean e.p.s.p.	Mean no. axons
23.1 ± 1.0	3.7 ± 0.2	6.5 ± 0.9	1.9 ± 0.1
Depolarization/axon = 6.2 mV		Depolarization/axon = 3.4 mV	

innervated by *both* T1 and T4, and receiving their strongest innervation (by the criterion of e.p.s.p. amplitude) from one or the other of these segments (150 of 912 neurones studied). If the strength of innervation of ganglion cells were a function of spinal cord position, then the average synaptic contribution of each axon from the dominant spinal segment should be greater than the average contribution of each non-dominant axon. Conversely, if all the axons contacting a ganglion cell were drawn to it with equal affinity, then the average synaptic contribution of each axon from dominant and non-dominant segments should be about the same. A rough measure of the average synaptic influence of axons on each cell from dominant and non-dominant levels was obtained by dividing the e.p.s.p. amplitude elicited in response to ventral root stimulation by the estimated number of innervating axons arising from that segment. The result of this comparison was that the average contribution of each axon from dominant segments was about twice as great as the average synaptic contribution made by each non-dominant axon (Table 2). This result suggests that the location of preganglionic neurones along the rostro-caudal axis of the spinal cord is, in fact, correlated with the affinity of their axons for ganglion cells.

DISCUSSION

The experiments we report here have explored the basis of selective innervation in the superior cervical ganglion. Our results are most easily explained by a synaptic selectivity which correlates positional attributes of the pre- and post-synaptic neurones. For ganglion cells, the relevant position appears to be that of peripheral targets, while for preganglionic neurones it is position along the rostro-caudal axis of the spinal cord.

The results that support the correlation of segmental innervation and post-ganglionic target position are:

1. End-organs with the same function tend to be activated by different spinal segments if they occupy different positions in the superior cervical territory.
2. End-organs with different functions at the same position tend to be activated by the same thoracic segments.
3. Post-ganglionic axons running to different destinations within the territory of the superior cervical ganglion arise from neurones whose segmental input differs in a systematic way.

The mechanism accounting for this correlation of pre- and post-synaptic positional attributes apparently does not discriminate in any absolute sense. Thus the tendency to make appropriate segmental connexions may be over-ridden after partial denervation and sprouting since end-organs can then be activated by inappropriate spinal levels (Murray & Thompson, 1957). Moreover, ganglion cells are readily re-innervated by entirely foreign axons (see, for example, Purves, 1976). These results suggest that the segmental innervation of a ganglion cell may normally reflect a compromise between the tendency to match positional values and the availability of preferred axons.

Correlating positional attributes of the pre- and post-synaptic neurones is unlikely to be the only criterion for the selective innervation of ganglion cells. For example, circumstantial evidence suggests that the function of pre- and post-synaptic cells provides a further basis for selective ganglionic connexions (see Purves & Lichtman, 1978, for discussion and references). Since selectivity according to function (or some other criterion) must be expressed through the same synaptic endings as the selectivity we have described here, the innervation of ganglion cells may be considerably more precise than indicated by our experiments.

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